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NOTES ON THE FLORAL GLANDS IN
TRIBULUS (ZYGOPHYLLACEAE)¹

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ABSTRACT

Morphology of the intrastaminal floral glands in *Tribulus* has been thought to be species-specific. However, this specificity breaks down in the Galápagos Islands. It is hypothesized that the breakdown there is due to interspecific hybridization between *T. cistoides* and *T. terrestris*.

Tribulus L. is an Old World genus of several dozen species. Most species are weedy occupants of dry disturbed habitats, either natural or man-induced. The yellow-flowered *T. cistoides* L. and *T. terrestris* L. have been distributed around the world by man, their spiny mericarps providing an ideal mechanism for dissemination. *Tribulus cistoides* is native to tropical and subtropical southern Africa.³ It is now a weed throughout the drier tropics, occurring mainly in maritime habitats. *Tribulus terrestris* is native to the Mediterranean region. It is a wide-spread weed in the warm-temperate areas of the world, occurring on all continents but Antarctica. It has been collected rarely in the tropics, then mostly at higher elevations. The ranges of *Tribulus cistoides* and *T. terrestris* are known to overlap only in two areas. One is in southern Africa; the second is in the Galápagos Islands, Ecuador.

One of the principal diagnostic floral characters distinguishing *Tribulus* from the closely-related genus *Kallstroemia* Scop., with which it is often confused, is the presence of a whorl of five intrastaminal glands at the base of the ovary in *Tribulus*. Intrastaminal glands are lacking in *Kallstroemia*, although both genera

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³*Tribulus zeyheri* Sond. is the name often used for the species in this area, especially in older works; *T. cistoides* was long considered to be a New World species. However, examination of a large number of specimens from both areas shows the range of morphological variation in the large-flowered *Tribulus* of each to be identical, notwithstanding Launert's (1963) attempt to separate two species in Africa. *Tribulus zeyheri*, therefore, is a synonym of the older name, *T. cistoides*.

have a whorl of five bilobed *extrastaminal* glands. In *Tribulus* both *extrastaminal* and *intrastaminal* glands are located next to or perhaps are continuous with the floral disc.

The disc and the *extrastaminal* and *intrastaminal* glands of *Tribulus cistoides* are all nectariferous, with the *extrastaminal* glands producing most of the nectar (Brown, 1938). The *extrastaminal* glands in *T. longipetalus* Viv.⁴ (as *T. alatus* Del.) and *T. terrestris* are not supplied by vascular bundles, and have been regarded as "stipular in nature" (Nair & Nathawat, 1958: 174). Apparently the *intrastaminal* glands also lack a vascular supply, as does the disc (*op. cit.* 179). Whether the glands represent reduced stamens or other organs or are organs which have arisen *de novo* is not clear. As floral glands and staminal appendages abound in the Zygophyllaceae, their study should provide a fertile field for anatomical research.

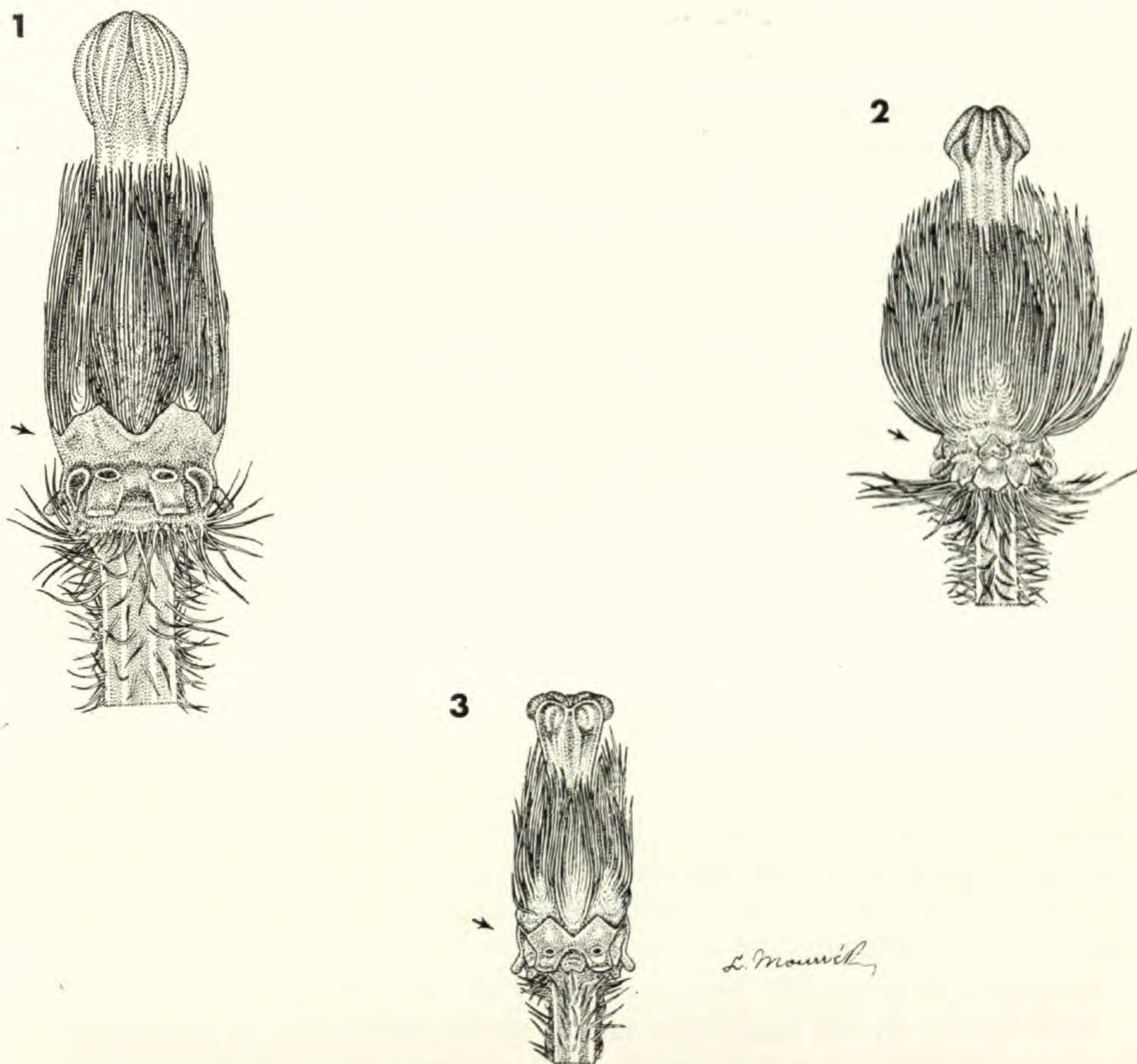
In his admirable study of *Tribulus* in South Africa, Schweikerdt (1937) has indicated the usefulness of the *intrastaminal* glands as a taxonomic character in the genus. He was the first to point out that the morphology of the *intrastaminal* glands does not vary within a species. The *intrastaminal* glands are triangular and free in *T. longipetalus* (as *T. alatus*), *T. macropterus* Boiss., and *T. terrestris* (Schweikerdt, 1937) and connate into a five-lobed urceolate ring surrounding the ovary base in *T. cistoides* (Schweikerdt, 1937, as *T. zeyheri*; Brown, 1938), *T. cristatus* Presl, *T. excrucians* Wawra, *T. pterocarpus* Ehrenb., and *T. pterophorus* Presl (Schweikerdt, 1937). In *Tribulopsis solandri* R. Br. (*Tribulus solandri* (R. Br.) F. Muell.), a member of an endemic Australian genus closely allied to *Tribulus*, they are bilobed and basally connate (Porter, 1969).

Following Schweikerdt's lead, others have found this character useful in keys for the identification of *Tribulus* species (Launert, 1963; Schreiber, 1966; Porter, 1967, 1970). *Intrastaminal* gland morphology seems to be consistent throughout the ranges of most species examined. However, a study of the genus in the Galápagos Islands (Porter, 1971) has revealed a breakdown in the species-specificity of the character. Here, the *intrastaminal* glands of *T. cistoides* are connate, the usual situation, while those of *T. terrestris* may be either free, as usual, or connate.

The morphology of the *intrastaminal* glands of those collections of *Tribulus* from the Galápagos Islands cited below has been determined as indicated.

1. *Tribulus cistoides* (*intrastaminal* glands connate).—Fig. 1.
 LOCALITY UNKNOWN: Snow 92 (DS).
 ISLA BALTRA: Howell 9952 (CAS).
 ISLA CHAMPION: SW slopes of old crater, Wiggins & Porter 511 (CAS, MO).
 ISLA DAPHNE MAJOR: Dawson, 1964 (DS, MO).
 ISLA ESPANOLA: Snodgrass & Heller 743 (DS, GH).

⁴ Gruenberg-Fertig and Zohary (1970) have shown that this name takes precedence over the well-known *Tribulus alatus*. Not only is the latter name illegitimate as they indicate, having been published with an older name applicable to a different species in its synonymy, it is also a *nomen nudum*, being published without a description. Accordingly, *T. longipetalus* is the name to be applied to the North African and Middle Eastern species, originally cited by the author as *T. alatus* (Porter, 1967), that has been introduced into Peru.



FIGURES 1-3. Intrastaminal gland morphology in *Tribulus*, $\times 12\frac{1}{2}$.—1. *T. cistoides* (intrastaminal glands connate).—2. *T. terrestris* (intrastaminal glands free).—3. *T. terrestris* (intrastaminal glands connate). (1. After Wiggins & Porter 511. 2. After Andersson, 1852. 3. After Wiggins 18702. All MO.)

ISLA FLOREANA: Near shore and in open places in vegetation, Stewart 1725 (CAS); cinder ridge ca. 2 km inland from E end of Post Office Bay, Wiggins & Porter 543 (CAS, MO); sand dunes at Cormorant Bay, Wiggins & Porter 561 (CAS, MO).

ISLA GENOVESA: Plateau above "Phillip's steps," Eisendrath, 1969 (MO).

ISLA ISABELA: Tagus Cove, near beach on sandy hillsides, Snodgrass & Heller 165 (DS), in tufaceous soil on tops and sides of hills surrounding cove, Stewart 1730 (CAS, GH, MO), side of cinder ridge 200 m NE of landing, Wiggins & Porter 240 (CAS, MO), landing at head of cove, Wiggins & Porter 241 (CAS, MO); Villamil, Howell 8935 (CAS, MO), in light ashy soil near sea level, Stewart 1722 (CAS, GH, MO).

ISLA SAN CRISTOBAL: Punta Pitt, Snow 255 (DS); Wreck Bay, Wiggins & Porter 446 (CAS, MO).

ISLA SANTIAGO: Sullivan Bay, Howell 10023 (CAS).

ISLA SANTA CRUZ: Along trail from Academy Bay to Bella Vista, Fosberg 44757 (MO, US), Wiggins 18431 (DS, MO), Wiggins & Porter 705 (CAS, MO).

ISLA TORTUGA: Stewart 1723 (CAS, GH).

2. *Tribulus terrestris* (intrastaminal glands free).—Fig. 2.

LOCALITY UNKNOWN: Andersson, 1852 (MO).

ISLA ESPANOLA: Gardner Bay, Howell 8658 (CAS).

ISLA FLOREANA: Post Office Bay, Howell 8805 (CAS).

3. *Tribulus terrestris* (intrastaminal glands connate).—Fig. 3.

ISLA FLOREANA: Among rocks along shore, *Stewart 1732* (CAS); Black Beach, *Howell 8913* (CAS).

ISLA SANTA CRUZ: Sand dunes 3 miles W of Academy Bay, *Taylor TT100* (CAS); slopes of dunes on lava peninsula along S shore of Tortuga Bay, *Wiggins 18702* (DS, MO).

Nineteen additional collections of *Tribulus cistoides* and one of *T. terrestris* from the archipelago were examined, but these were either sterile or too scrappy to determine as to gland morphology.

The yellow flowers of *Tribulus cistoides* and *T. terrestris* superficially differ mainly in size. Those of *T. cistoides* generally are 20–40 mm in diameter, while those of *T. terrestris* are 5–10 mm in diameter. In the Galápagos Islands, however, the flowers of *T. cistoides* vary from 15–25 mm in diameter. Such wide variation in *T. cistoides* has also been observed in Mexico, where specimens have been collected whose petals vary in size from 8 × 5 mm [PUEBLA: 5 miles NE of Tehuacán, *Porter 1448* (GH, MEXU, MO)] to 21 × 12 mm [VERA CRUZ: Vera Cruz, *Porter 1460* (DS, GH, MEXU)]. A parallel variation exists in the size and the amount of pubescence of the vegetative parts in this species. Plants of *T. cistoides* growing under more extreme ecological circumstances (such as in the open along the edge of a well-traveled road, or in an area subject to the salt spray of the sea) have smaller flowers and leaves, shorter internodes, and are heavily pubescent. Those growing under more favorable circumstances have larger flowers, longer internodes, and less pubescence. Collections of the former type from the Galápagos Islands, the most common phenotype of collections of this species examined from the archipelago, have been described as *Tribulus sericeus* Anderss. Such polymorphism in the genus has led to many problems in specific delimitation (Schweikerdt, 1937; Launert, 1963; Squires, 1969).

Both species in the Galápagos bloom at the same time of year, following the rains. The flowers of *Tribulus cistoides* are protandrous (Robertson & Gooding, 1963), and those of *T. terrestris* are protogynous (Goldsmith & Hafenrichter, 1932). Individual flowers, then, are usually outcrossed; thus the possibility of interspecific hybridization exists. Schweikerdt (1937) has hinted at such hybridization, but so far as I am aware, neither natural nor artificial interspecific hybridization has been demonstrated in *Tribulus*.

Few pollinating insects are known from the Galápagos Islands. Among potential insect pollinators are butterflies, moths, flies, beetles, wasps, an ant, and a bee (Linsley, 1966). However, with one exception, little is known regarding their relationships to pollination. The one exception is *Xylocopa darwini* Cockerell, the endemic Galápagos carpenter bee. *Xylocopa darwini* "is undoubtedly the principal pollen vector associated with plants of the Galapagos flora" (Linsley *et al.*, 1966: 1). It has been observed visiting a wide variety of plants, including 63 species in 28 families (Rick, 1963, 1966; Linsley *et al.*, 1966), for both pollen and nectar. From my personal observation, many of these are yellow-flowered. *Xylocopa darwini* is "common and widely distributed in the archipelago, chiefly at low elevations and along sea beaches" (Linsley, 1966: 226). This describes precisely the habitat of *Tribulus* on the islands, and *X. darwini*

has been observed visiting the flowers of *T. cistoides* at Academy Bay, Isla Santa Cruz (Linsley *et al.*, 1966).

In light of the above information, an hypothesis can be proposed to explain the presence of connate intrastaminal glands in several collections of *Tribulus terrestris* from the Galápagos Islands. The condition is the result of gene-exchange between small-flowered individuals of *T. cistoides* and *T. terrestris*, accomplished through pollen carried from one to the other by the carpenter bee, *Xylocopa darwini*. Introgression of genes from *T. terrestris* into *T. cistoides* may also explain the high proportion of small flowers in the latter species as found in the archipelago.

It is interesting to note that in southern Africa, the other area where these two species are known to overlap in range, there is no indication of hybridization between them. Smaller-flowered individuals of *Tribulus cistoides* are rare in southern Africa; they are common in the Galápagos Islands. Accordingly, the opportunities for hybridization in Africa must be few. The presence of a common, wide-ranging pollinator in the Galápagos Islands has increased such opportunities many-fold. Unfortunately, nothing is known of the African pollinators of *Tribulus*.

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